

DIFFERENTIAL USE OF THE HABITAT BY *PARDOSA PULLATA* (CLERCK) AND *PARDOSA PRATIVAGA* (L. KOCH) IN A MIXED POPULATION (ARANEAE, LYCOSIDAE)

by

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ABSTRACT

The distribution of *P. prativaga* and *P. pullata* in a mixed population is studied in relation to structural characteristics of the vegetation. The results are discussed in the context of the possibility of the occurrence of interbreeding between the species studied.

ACKNOWLEDGEMENTS

The authors wish to thank Prof. Dr. L. Vlijm for his valuable criticism during the investigation and the preparation of the manuscript. They are also highly indebted to all the workers of the Biologisch Station "Weevers' Duin", Oostvoorne and the "Vereniging tot Behoud van Natuurmonumenten in Nederland", which made it possible to undertake this study; to Mr. G. W. H. van den Berg, for the drawing of the graphs, and to Miss P. G. Brink, for the typing out of the manuscript.

INTRODUCTION

The systematics of the species of the *Pardosa pullata* group are rather confusing. Several authors have described a number of species, under various names, within this group (Locket & Millidge, 1951; Wiebes, 1959; Tongiorgi, 1966; Holm & Kronestedt, 1970). The characters, on which the systematics of the Lycosidae generally are based, almost exclusively concern external morphological features, viz., the colour and design of the body, the spinosity of the legs and the shape of the external genitalia. However, the frequency distributions of a number of measurements of these characters in species of the *Pardosa pullata* group overlap considerably. Several of the measured characters vary to a rather large extent between populations of the same species; especially the data of mixed populations differ from those of pure populations (Den Hollander, 1970). On the basis of these results, as well as of the occurrence of intermediate specimens in mixed populations, the possibility of interbreeding in the field has been assumed (Locket & Millidge, 1951; Den Hollander, 1970). A study of the phenology of the species *Pardosa pullata*, *P. prativaga* and *P. sphagnicola* has shown that seasonal barriers generally prevent interbreeding in mixed populations, but that in some years, because of weather conditions during spring, these barriers are broken down (Den

Hollander, 1971). In addition, under laboratory conditions hybrid specimens have been obtained from interspecific breedings between *P. pullata*, *P. prativaga*, and *P. sphagnicola* (Den Hollander, in prep.).

However, the occurrence of interbreeding in the field is also dependent on the occurrence of habitat isolation between the species. When two species, occurring in mixed populations, use different parts of the habitat, they will not meet and thus interbreeding will be prevented. Richter et al. (1971) studied the locomotory activity of both *P. pullata* and *P. prativaga* in pure, as well as in mixed populations during the reproductive period. They found that this activity of *P. prativaga* males was much higher than that of *P. pullata*; the locomotory activity of females was of the same level in both species, this level being considerably lower than in the males. Richter (1970) studied the relation between the structure of the habitat in which the species occurs, the quantity of silk produced, the orientation of the plane in which the silk is spun, and the degree of development of the glandulae ampullaceae. He found that species living in a field-type vegetation (e.g. *Pardosa prativaga*) have large glandulae ampullaceae, produce larger quantities of silk, and spin proportionally more silk in the vertical plane, while the converse is true for species from the open ground-type vegetation (e.g. *P. pullata*).

These results suggest a differential use of the habitat by *P. prativaga* and *P. pullata*. The aim of the present study is to investigate the distributions of *P. pullata* and *P. prativaga* in a mixed population in relation to structural characteristics of the vegetation, in order to establish the differences between the species in more detail. At the same time this study is undertaken with a view to discussing the fore-mentioned differences in relation to the possibility of interbreeding of the species (cf. Den Hollander, 1970, 1971).

MATERIAL AND METHODS

The study area is a yearly mown meadow, primarily grown with *Lysimachia vulgaris* L., *Hydrocotyle vulgaris* L., moss carpets (*Polytrichum* spec.) and various grasses and sedges (Table 1). It is situated in a dune valley near Rockanje in the southwestern part of the Netherlands. In autumn and winter the field is very wet. It appeared that the water content of the soil was about 50% throughout the study area. However, at the

Table 1. The percentages cover of the occurring plant species in the high growing herb layer (K1) and the low growing herb layer (K2) of the vegetation in the study area

	Plant species	Percentage cover
High growing herb layer (K1)	<i>Lysimachia vulgaris</i>	65
	<i>Eupatorium cannabinum</i>	10
	<i>Lycopus europaeus</i>	5
	<i>Salix repens</i>	10
	<i>Scutellaria galericulata</i>	0—5
Low growing herb layer (K2)	<i>Hydrocotyle vulgaris</i>	60
	<i>Rubus</i> spec.	30
	<i>Calamagrostis</i> spec., <i>Carex arenaria</i> , <i>C. nigra</i> , <i>C. disticha</i>	30
	<i>Potentilla anserina</i> , <i>P. erecta</i> , <i>P. reptans</i>	10
	<i>Polytrichum</i> spec.	0—100
	Litter	0—50

borders, where the ground level was about 30—50 cm higher than in the centre, the water content was about 25% (data of May, 1970).

Throughout the study area 68 pitfall traps (diameter 10 cm) were placed (Fig. 1), in such a way that the upper margin of the jars was just level with the surface of the soil. The jars were filled with formalin (4%) to which some detergent was added. In these traps spiders were caught on three days (during 24 hours), between May 28 and June 8. In the same period 10 catches by hand were carried out on five days, two catches of 80 minutes each day.

The structural characteristics of the vegetation were described on the basis of the percentage cover, the total height and the species composition (Tables 5 and 6). Two types of herb layer were distinguished, viz., (Table 1) a low growing herb layer and a high growing herb layer. The high layer mainly consisted of *Lysimachia*, in the low growing type *Hydrocotyle* was the dominant plant species. In this study, litter is considered a component of the low growing herb layer, so that the complement of the

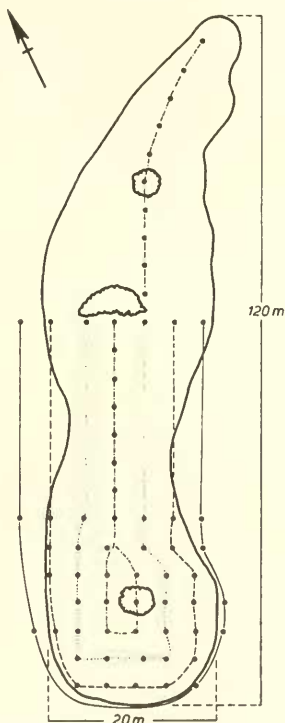


Fig. 1. The location of the 68 pitfall traps in the study area; —, — — —, ..., — · —, — — — —, correspond to locality 1, 2, 3, 4 and 5 of Table 4, respectively)

percentages cover consists of bare ground. With the help of these characteristics four types of differently structured vegetation will be shown to occur in the study area: vegetation of a low open type (LO), a low dense type (LD), a high open type (HO) and a high dense type (HD).

The numbers of spiders (males, females and females carrying egg sacs) per pitfall trap in the respective types of vegetation will be compared. The numbers of juveniles were not taken into account, because only small numbers were caught.

RESULTS

For both species the total numbers per category caught in the pitfall traps over the whole study area are presented in Table 2. It shows that most of the spiders collected were males (about 80%). *P. prativaga* was caught in the traps slightly more frequently than *P. pullata*. From the females of *P. pullata* 44% were carrying an egg sac, whereas this percentage amounted to 28% in *P. prativaga*.

The numbers of spiders (per category) caught by hand are presented in Table 3, showing that less than 20% were males (traps: 80%), largest numbers being females carrying an egg sac (*prativaga*: 58%; *pullata*: 80%). Whereas in pitfall traps both species were caught in about equal numbers (Table 2), with hand sampling the numbers of *P. prativaga* amounted to less than 30% of the total number. Thus rather striking differences exist between the composition of the sample obtained by hand sampling (Table 3) and that by pitfall trapping (Table 2).

Table 2. The total numbers of both species per category caught in 68 pitfall traps over the whole study area (♀ c stands for ♀ with egg sac)

Species	Category				% ♂ of total	% ♀ c of total ♀
	♂	♀	♀ c	total		
pullata	280	49	39	368	76	44
prativaga	414	63	25	502	82	28

Total: 870, % *prativaga* of total: 58

These differences illustrate that the two methods of sampling give different results as to the composition of the population. With hand sampling spiders seen by the catcher, i.e. those sitting or walking slowly upon a not too high vegetation, are caught. On the other hand, spiders running on the ground or low in the vegetation are more easily caught in pitfall traps: the higher the locomotory activity, the higher the chance to be caught. Thus, when comparing Tables 2 and 3, it appears that males show the highest locomotory activity of all categories, whereas females carrying an egg sac are the least

Table 3. The total numbers of both species per category caught by hand over the whole study area (♀ c stands for ♀ with egg sac)

Species	Category				% ♂ of total	% ♀ c of total ♀
	♂	♀	♀ c	total		
pullata	92	94	380	566	16	80
prativaga	38	72	100	210	18	58

Total: 776, % *prativaga* of total: 27

active. In addition, females carrying an egg sac more often occur upon the herb layer than males.

The different percentages of *P. prativaga* in both samples are more difficult to explain, since the real densities of both species are not known. However, Richter et al. (1971) found that, during short periods, the straight line distance covered by *P. prativaga* males was about 3.5 times as long as that of *P. pullata* males (these data were collected in the present study area). Thus, other factors being equal, the chance that a male of *P. prativaga* is caught in a trap will be about 3.5 times as great as for a *P. pullata* male. On the basis of the figures in Table 2 the ratio of the number of males of *P. pullata* to that of *P. prativaga* is 2.4 ($280 : (414 : 3.5) = 2.4$). As exactly the same proportion is found in hand sampling (Table 2, $92 : 38 = 2.4$) it may be concluded that males of both species use the habitat in the same way; in other words the chance to be caught is a function of the locomotory behaviour rather than of the way in which the habitat is used.

The distributions of both species throughout the study area as established with the help of pitfall trapping are presented in Table 4. The distribution of the traps in the study area is given in Fig. 1.

Table 4 shows that both species occur throughout the meadow but that they scarcely occur in locality 1, i.e. the surrounding shrubs and trees. For both species the numbers of specimens are largest in locality 5. In the localities 2–5 the percentage of males of the total catch amounts to the same. Thus both *P. prativaga* and *P. pullata* occur especially in the northeastern part of the meadow (see Fig. 1), but the percentage of *P. prativaga* slightly decreases from locality 2 towards locality 5. The reason may be that towards the northeastern part of the meadow the proportion of the vegetation type LO (see below) increases.

Table 4. The distributions of both species per category throughout the study area: —, locality 1; — — —, locality 2; . . ., locality 3; — — — —, locality 4; — — — — —, locality 5 (cf. Fig. 1).

Locality (see Fig. 1)	Number of traps	Numbers of spiders per 10 traps									
		<i>prativaga</i>					<i>pullata</i>				
		♂	♀	total	% ♂ of total		♂	♀	total	% ♂ of total	% <i>prativaga</i> of total spiders
1	9	6	—	6	100		6	—	6	100	50
2	18	58	11	69	84		25	10	35	71	66
3	16	68	17	85	80		49	14	63	78	58
4	15	64	16	80	80		44	19	63	70	56
5	10	94	17	111	85		78	19	97	80	54

The results suggest that the factors determining distributions of both *P. prativaga* and *P. pullata* are essentially the same. If this is true, a positive correlation of the numbers of *P. prativaga* and those of *P. pullata* per trap may be expected. The linear correlation coefficient (r) appeared to be 0.44, which is statistically significant at $\alpha = 0.01$ ($n = 68$). Thus, when in one of the 68 traps, i.e. on a certain place in the study area, larger or smaller numbers of *P. prativaga* occur than in another trap, the same is true for *P. pullata*.

The percentages cover of the high growing (K1) and low growing (K2) herb layer, as well as the total height of the vegetation (H) for the four vegetation types (cf. Methods), are presented in Table 5.

It is evident that in type LO the vegetation is poorly developed, predominantly with low grown plants. Vegetation type LD differs from LO in that, especially, the cover of the low growing herb layer is higher. In type HO the vegetation grows higher than in LD and LO, the percentage cover of the high growing herb layer being slightly higher, that of the low growing herb layer slightly lower, as compared to vegetation type LD. Thus the influence of sunshine and wind-velocity on the microclimate will be less in vegetation type HO than in LO and LD. In type HD the vegetation is densely structured:

Table 5. Percentages cover of the high growing herb layer (K1), the low growing herb layer (K2) and the total height of the vegetation in the four types

Type	% K1	% K2	H
LO	8 (2—20)	36 (5—50)	20 (15—25)
LD	24 (15—25)	74 (70—80)	25 (20—30)
HO	31 (25—40)	60 (55—65)	37 (30—50)
HD	82 (75—95)	81 (70—90)	41 (30—50)

both the low growing and the high growing herb layers cover the ground to a large extent. Thus the microclimate will be strongly stabilized against the influence of sunshine and wind-velocity. The total height of the vegetation consequently separates the low types (LO and LD) from the high types (HO and HD). Within the low types there is a separation on the account of the low growing herb layer, in the high types, on that of the high growing.

The mean values for the percentages of cover of several plant species in the respective vegetation types are presented in Table 6. The values were obtained in the following manner. First, the vegetation type in the direct surroundings of every pitfall trap was established. Next, the percentages cover of the respective plant species in each of the 68 localities was valued in a range of 0—10 (for moss only the presence or absence was recorded, indicated by 1 or 0, respectively).

Table 6 shows that in the low vegetation types (LO and LD) *Hydrocotyle* is the predominant plant species, while in the high vegetation types (HO and HD) *Lysimachia* predominates. In the open types (LO and HO) the litter component is larger than in the densely structured types (LD and HD), whereas in the latter the grass component is larger than in the former. Thus, in type LO *Hydrocotyle* and litter are the most important components. In type LD, as compared with type LO, the components *Lysimachia* and moss have higher values, the component litter being considerably smaller. The component *Lysimachia* again is larger in the types HO and HD. In type HD the component grass is larger and the component *Hydrocotyle* smaller than in all other types. Thus it may be concluded that the four vegetation types differ both in structure (Table 5) and species composition (Table 6).

The results of some measurements of microclimatological characteristics (temperature, humidity) are illustrated in Fig. 2. The values presented were taken with an Asmann psychrometer during bright, sunny weather.

Fig. 2 shows that at a certain temperature of the air at a height of 2.00 m, the temperature at the ground level is highest in type LO, while the lowest temperature is

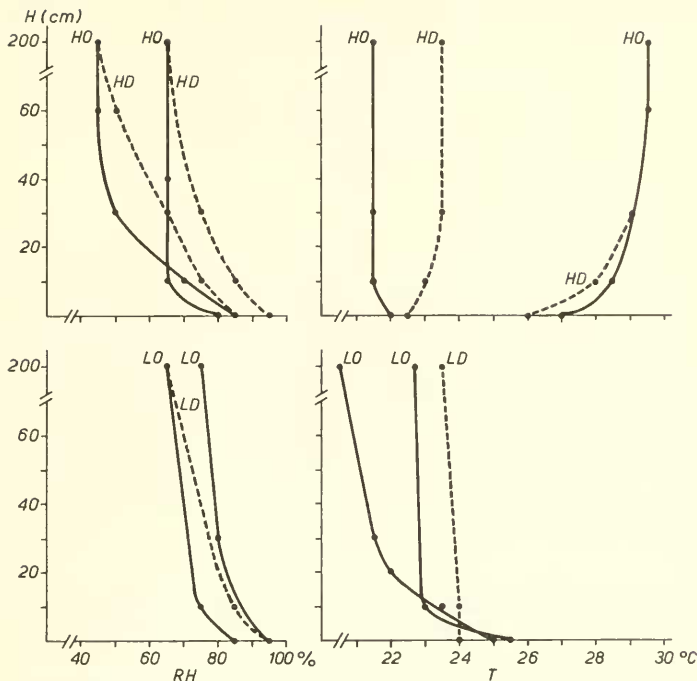


Fig. 2. Microclimatological characteristics (temperature, T and humidity, RH) in the various types of vegetation (above: high types; below: low types)

recorded in type HD. The differences between air temperature and ground temperature in the high vegetation types is larger when the air temperature is higher. In the low vegetation types these differences are smaller.

In all types of vegetation, the relative humidity appears to be highest at the ground level, the value being slightly higher in the densely structured vegetations, as compared with the open structured ones. Especially in the high vegetations (HO, HD) the difference between the relative humidity at the 2.00 m level and at the ground level is higher, when the relative humidity at the 2.00 m level is lower.

It may be concluded that the structure of the vegetation exerts an influence on the microclimate, which therefore differs between the respective types (LO, LD, HO and HD). Especially when wind velocity and clouding become important factors, they will modify the microclimate. The above mentioned differences will then become more important.

The mean numbers of spiders per trap caught in each of the vegetation types are shown in Table 7. The largest numbers, both of *P. prativaga* and *P. pullata*, were caught

Table 6. The mean values for the cover of several plant species in the different types of vegetation (cf. text)

Type	Plant species					Number of traps
	Lysimachia	Hydrocotyle	Grasses and Sedges	Moss	Litter	
LO	2.0	4.0	2.0	0.3	2.2	13
LD	4.3	4.9	2.7	0.6	1.5	20
HO	5.6	4.0	2.0	0.2	2.0	11
HD	5.3	3.2	3.3	0.0	1.5	15

in the dense vegetation types (LD and HD), the numbers in HD being larger than in LD. In both types the percentage of *P. prativaga* in the samples amounts to about 60 %. In the open vegetation types (LO and HO) the total number of spiders is the same, the numbers of *P. prativaga*, however, are lower in LO than in the other three vegetation types, whereas the numbers of *P. pullata* in LO are the highest, except those in HD. This is reflected in the percentage of *P. prativaga* in the samples, which also is about 60 % in type HO (as in LD and HD) but only 40 % in vegetation type LO.

Throughout the series LO, HO, LD and HD the percentages of the cover of the low growing herb layer increase (Table 5), as do the values for the cover of grasses and sedges, whereas those of the litter decrease throughout the series (Table 6). The numbers of *P. prativaga* increase gradually from LO through HO and LD towards HD (Table 7), i.e. the numbers of *P. prativaga* are correlated with the cover of the low growing herb layer, grasses, sedges and litter. The same is true for *P. pullata* in the series HO, LD, HD. In LO more specimens of *P. pullata* were caught than could be expected on the basis of the correlation, mentioned above.

More information may become available when the respective categories of spiders are analysed. Table 8 presents the mean numbers per category of both species caught in the four types of vegetation, per pitfall trap.

Table 7. The mean numbers of both species per trap in the different types of vegetation

Type	Species			
	<i>prativaga</i>	<i>pullata</i>	Total	% <i>prativaga</i> of Total
LO	4.2	7.0	11.2	40
LD	9.2	5.9	15.1	60
HO	7.6	4.3	11.9	61
HD	11.7	7.2	18.9	62

Although only a small number of females was caught, for both species the numbers, in percentages of the total, were slightly lower in type LO than in the others. In addition, only 6 % of the females of *P. pullata* caught in type LO carried an egg sac, whereas this percentage was 50—60 % in the other vegetation types. In *P. prativaga* 23—33 % of the females were with egg sac in all the vegetation types. Thus the higher numbers of *P. pullata* in vegetation type LO are only caused by the higher numbers of males and females without egg sac.

In *P. prativaga* the relative proportions of the three categories of spiders is the same in the different types of vegetation, their numbers increasing from LO — HO — LD

Table 8. The mean numbers of both species (per category) per trap in the different types of vegetation (♀ c stands for ♀ with egg sac)

Type	Species									
	<i>prativaga</i>					<i>pullata</i>				
	category									
	♂	% ♂ of total	♀	♀ c	% ♀ c of total ♀	♂	% ♂ of total	♀	♀ c	% ♀ c of total ♀
LO	3.6	87	0.4	0.2	29	5.7	82	1.2	0.1	6
HO	6.5	85	0.8	0.4	30	3.2	74	0.5	0.6	58
LD	7.5	81	1.4	0.4	23	4.3	73	0.8	0.9	53
HD	9.5	81	1.5	0.7	33	5.3	74	0.9	0.9	50

— HD. Concerning males and females without an egg sac, there are differences between *P. pullata* and *P. prativaga*, the numbers of the former increasing from HO — LD — HD — LO. Females of *P. pullata* carrying an egg sac hardly occur in vegetation type LO. Thus, in *P. prativaga* the largest numbers of the three categories of spiders occur in vegetation type HD, i.e. this vegetation type is preferred by males as well as by females, both with and without an egg sac. The same holds true for females of *P. pullata* with egg sacs. However, in this species males and females without an egg sac prefer vegetation type LO.

CONCLUSIONS

Of the numbers of both *P. prativaga* and *P. pullata*, taken by pitfall traps 80% are males. In *P. prativaga* 30 % of the females carry an egg sac, in *P. pullata* about 40 %. The numbers of *P. prativaga* amount to about 60 % of the total numbers caught. However, in the samples taken by hand, males account for only 20 % of the numbers caught, in *P. prativaga* as well as in *P. pullata*. 60 % of the females of *P. prativaga* and 80 % of the females of *P. pullata* carry an egg sac. In this sample only 30 % of the spiders belong to *P. prativaga*.

The difference in composition between the samples taken by pitfall traps and those taken by hand sampling reflects that females carrying an egg sac, as compared with both females without egg sac and males, show the lowest locomotory activity and occur more upon the vegetation. The different percentages of *P. prativaga* in the different samples are mainly caused by the higher activity of *P. prativaga*, as compared with *P. pullata*.

Both *P. prativaga* and *P. pullata* occur throughout the investigated area. Towards the northeastern part of the field the numbers of both species increase, in *P. pullata* to a larger extent than in *P. prativaga*.

Four different vegetation types, distinguished on the basis of their structure, occur in the study area. They are defined by the height and species of the composing plants, as well as by the percentages cover of both the low growing and high growing herb layers. As a consequence, the microclimatological conditions differ between the various vegetation types (LO, LD, HO, HD).

Both *P. prativaga* and *P. pullata* occur in all types of vegetation. In *P. prativaga* the numbers of males and females without an egg sac increase gradually from LO — HO — LD — HD; in *P. pullata*, on the contrary, from HO — LD — HD — LO. In both

species the numbers of females carrying an egg sac increase from LO — HO — LD — HD. Thus the preferred vegetation type for males and females of *P. prativaga*, as well as for females of *P. pullata* carrying an egg sac, is the high, densely structured vegetation (HD), and for males and females without an egg sac of *P. pullata*, the low, open structured type (LO).

DISCUSSION

Former studies (Den Hollander, 1970, 1971) showed that in mixed populations interbreeding between *P. prativaga* and *P. pullata* might occur in some years. In those particular years, characterized by a cold spring, the seasonal barriers between both species are broken down. Laboratory studies showed that males of *P. prativaga* mate with females of *P. pullata* which results in living offspring. On the other hand, males of *P. pullata* do not mate with females of *P. prativaga* (cf. Den Hollander, 1972). Thus, interbreeding between the species studied under natural conditions can occur in only one direction, at least when both categories of spiders meet, i.e. when they are not isolated by a differential use of the habitat in mixed populations.

The results of the present study show that both males and females of the species studied occur throughout the investigated area. Moreover, the numbers of *P. prativaga* caught per pitfall trap are positively correlated with those of *P. pullata*, and the differences between samples taken by hand and those taken by pitfall traps are similar in both species when the higher locomotory activity of *P. prativaga* males, as compared with males of *P. pullata*, is taken into account. Therefore, it may be concluded that males of the one species are not completely isolated from females of the other.

Nevertheless, some differences in habitat preference between both males, and females without an egg sac (i.e. receptive females) of *P. prativaga* and *P. pullata* could be established. The largest numbers of *P. pullata* were obtained in vegetations, poorly grown with low growing plants. *P. prativaga*, on the other hand, was caught in the largest quantities in vegetations, densely grown with high growing plants. Besides, these two types of vegetations clearly differ concerning the values for temperature and relative humidity of the microclimatic conditions, as compared with those of the macroclimate. In the first type of vegetation temperature at the ground level is higher than that in the second type, mainly by the more direct radiation of the sun in the former. The opposite is true for the relative humidity. On the other hand, the influence of wind velocity and clouding on the microclimate will be less in the densely grown vegetations as compared with the other types.

Probably, these results may be understood as a higher resistance to loss of water in *P. pullata*, as compared with *P. prativaga*. Indeed, unpublished observations in our laboratory showed that *P. pullata* survives at low humidities and high temperatures, for a much longer period than *P. prativaga*.

The results concerning the preferred types of habitat for both species agree with the description of the characteristics of the habitats of *P. pullata* and *P. prativaga* given by previous authors (Dahl, 1908; Palmgren, 1939; Tambs-Lyche, 1940; Nørgaard, 1945, 1951; Holm, 1947; Locket & Millidge, 1951; Wiebes, 1959; Tongiorgi, 1966; Vlijm & Kessler-Geschiere, 1967; Richter, Den Hollander & Vlijm, 1971; Den Hollander, 1971). According to these authors both species occur in moist fields overgrown to various extents. Especially Nørgaard (1945, 1951) mentions that *P. pullata* prefers localities

which are exposed both to direct radiation by the sun and to the influence of wind velocity. Several authors mention that *P. pullata* occurs in localities overgrown with low plants, whereas *P. prativaga* would occur in localities overgrown with high plants. In agreement with this, Richter et al. (1971) states that *P. pullata* is more adapted, measured in quantities of silk production, to open ground type vegetations and *P. prativaga* more to field type vegetations (see also introduction).

These differences between *P. prativaga* and *P. pullata* mostly are gradual. In comparing distinct populations, both species occur in wide, overlapping ranges of vegetation types. Nevertheless, in pure as well as in mixed populations, the two species show a tendency to diverge to some extent in their use of habitat. This tendency to diverge may be caused by interspecific competition between both, closely related, species. This tendency may be inhibited, however, by the occurrence of interbreeding, as complete isolation mechanisms do not seem to exist between the species studied.

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